University of Maine.

# Maine Agricultural Experiment Station

ORONO

BULLETIN 243 NOVEMBER, 1915

## FURTHER DATA ON THE MEASUREMENT OF INBREEDING

CONTENTS.

# MAINE AGRICULTURAL EXPERIMENT STATION ORONO, MAINE.

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# BULLETIN 243.

## FURTHER DATA ON THE MEASUREMENT OF INBREEDING.[1]

By Raymond Pearl.

The purpose of the present bulletin is to continue the discussion of the measurement of inbreeding beyond the point where it was left in Bulletin 215 of this Station.[2] In that bulletin,

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[1]This bulletin is based on certain technical studies on the theory of inbreeding which have appeared since the publication of Bulletin 215 of this Station. These technical papers have appeared under the general title "Studies on Inbreeding." The following list gives the bibliographical data regarding this series.

Studies on Inbreeding. I. A Contribution towards an Analysis of the Problem of Inbreeding. By R. Pearl, Amer. Nat. Vol. XLVII, pp. 577-615, 1913.

II. Tables for Calculating Coefficients of Inbreeding. By R. Pearl and John Rice Miner, Ann. Rept. Me. Agr. Expt. Stat. for 1913, pp. 191-202, (Bulletin 218), 1913.

III. On the Results of Inbreeding a Mendelian Population: A Correction and Extension of Previous Conclusions. By R. Pearl, Amer. Nat. Vol. XLVIII, pp. 57-62, 1914.

IV. On a General Formula for the Constitution of the *n*th Generation of a Mendelian Population in which all Matings are of Brother and Sister. By R. Pearl. *Ibid.* Vol. XLVIII, pp. 490-494, 1914.

V. Inbreeding and Relationship Coefficients. By R. Pearl. *Ibid.* Vol. XLVIII, pp. 513-523, 1914.

VI. Some Further Considerations regarding Cousin and Related Kinds of Mating. By R. Pearl. *Ibid.* Vol. XLIX, pp. 570-575, 1915.

It should be said that the above papers (with the exception of II) are not available for distribution by the Maine Agricultural Experiment Station. It is, however, the aim of the present bulletin, in conjunction with Bulletin 215 of this Station, to present the essential features of this series of studies likely to be of interest to the practical stock breeder in condensed form. A general review of the whole subject in detail will be found in the present writer's book entitled "Modes of Research in Genetics," New York (The Macmillan Co.) 1915.

[2]Pearl, R. The Measurement of the Intensity of Inbreeding. Me. Agr. Expt. Stat. Bulletin 215, pp. 123-138. 1913.

besides the general theory of the inbreeding coefficients and the practical means for their calculation, the consequences of continued brother $\times$ sister and parent $\times$ offspring breeding were discussed. Along the same line we shall now consider the theoretical consequences of

(a) Continued mating of first cousins, and

(b) Continued breeding of individuals exhibiting the avuncular type of relationship, that is, uncle $\times$ niece or nephew $\times$ aunt.

Another matter which will be discussed, as it was not considered at all in Bulletin 215, is the measurement of the proportionate part played in the total observed inbreeding by the fact that sire and dam are related to each other, as compared with inbreeding in the ancestry of either sire or dam alone.

## Cousin Mating.

There are two possible sorts of first cousins, single and double. In the first case one of the parents of any individual is a brother (or sister) to the one of the parents of the other individual in the mating. In the second case, both the parents occupy this relation to the parents of the other individual in the mating.

These two sorts of first cousinship are shown in Pedigree Tables I and II.

## PEDIGREE TABLE I (HYPOTHETICAL).

*To Illustrate the Continued Breeding of First Cousin × First Cousin — Single Cousins.*

| | | | | | |
|---|---|---|---|---|---|
| A | a | c | g | m | 1 |
| | | | | | 2 |
| | | | | n | 3 |
| | | | | | 4 |
| | | | h | o | 1 |
| | | | | | 2 |
| | | | | p | 5 |
| | | | | | 6 |
| | | e | i | m | 1 |
| | | | | | 2 |
| | | | | n | 3 |
| | | | | | 4 |
| | | | j | q | 1 |
| | | | | | 2 |
| | | | | r | 9 |
| | | | | | 10 |
| | b | d | g | m | 1 |
| | | | | | 2 |
| | | | | n | 3 |
| | | | | | 4 |
| | | | h | o | 1 |
| | | | | | 2 |
| | | | | p | 5 |
| | | | | | 6 |
| | | f | k | m | 1 |
| | | | | | 2 |
| | | | | n | 3 |
| | | | | | 4 |
| | | | l | u | 1 |
| | | | | | 2 |
| | | | | v | 7 |
| | | | | | 8 |
| Generation number | 1 | 2 | 3 | 4 | 5 |

PEDIGREE TABLE II (HYPOTHETICAL).

*To Illustrate the Continued Breeding of First Cousin × First Cousin — Double Cousins.*

| | | | | | |
|---|---|---|---|---|---|
| A | *a* | *c* | *g* | *k* | *o* |
| | | | | | *p* |
| | | | | *l* | *q* |
| | | | | | *r* |
| | | | *h* | *m* | *o* |
| | | | | | *p* |
| | | | | *n* | *q* |
| | | | | | *r* |
| | | *d* | *i* | *k* | *o* |
| | | | | | *p* |
| | | | | *l* | *q* |
| | | | | | *r* |
| | | | *j* | *m* | *o* |
| | | | | | *p* |
| | | | | *n* | *q* |
| | | | | | *r* |
| | *b* | *e* | *g* | *k* | *o* |
| | | | | | *p* |
| | | | | *l* | *q* |
| | | | | | *r* |
| | | | *h* | *m* | *o* |
| | | | | | *p* |
| | | | | *n* | *q* |
| | | | | | *r* |
| | | *f* | *i* | *k* | *o* |
| | | | | | *p* |
| | | | | *l* | *q* |
| | | | | | *r* |
| | | | *j* | *m* | *o* |
| | | | | | *p* |
| | | | | *n* | *q* |
| | | | | | *r* |
| Generation number | 1 | 2 | 3 | 4 | 5 |

TABLE I.

*Values of the Successive Coefficients of Inbreeding in the Case of Continued Cousin Mating.*

| Coefficient of Inbreeding | Ancestral Generation Included | Coefficient for Single Cousins | Coefficient for Double Cousins | Coefficient for Brother × Sister |
|---|---|---|---|---|
| $Z_0$ | 1 | 0 | 0 | 0 |
| $Z_1$ | 2 | 0 | 0 | 50.00 |
| $Z_2$ | 3 | 25.00 | 50.00 | 75.00 |
| $Z_3$ | 4 | 50.00 | 75.00 | 87.50 |
| $Z_4$ | 5 | 68.75 | 87.50 | 93.75 |
| $Z_5$ | 6 | 81.25 | 93.75 | 96.98 |
| $Z_6$ | 7 | 89.06 | 96.98 | 98.44 |
| $Z_7$ | 8 | 93.75 | 98.44 | 99.22 |
| $Z_8$ | 9 | 96.48 | 99.22 | 99.61 |
| $Z_9$ | 10 | 98.05 | 99.61 | 99.80 |
| $Z_{10}$ | 11 | 98.93 | 99.80 | 99.90 |
| $Z_{11}$ | 12 | 99.41 | 99.90 | 99.95 |
| $Z_{12}$ | 13 | 99.68 | 99.95 | 99.98 |
| $Z_{13}$ | 14 | 99.83 | 99.98 | 99.99 |
| $Z_{14}$ | 15 | 99.91 | 99.99 | 99.994 |
| $Z_{15}$ | 16 | 99.95 | 99.994 | 99.997 |

The values of the coefficients of inbreeding ($Z_0$ to $Z_{15}$) for continued single and double cousin matings are shown in Table I. These coefficients are calculated from the usual formula,

$$Z_n = \frac{100\,(p_{n+1} - q_{n+1})}{p_{n+1}} \qquad \text{(i)}$$

where $p_{n+1}$ denotes the maximum possible number of different individuals involved in the matings of the $n+1$ generation, $q_{n+1}$ the *actual* number of different individuals involved in these matings. The method of using this formula on a pedigree has been fully explained[3] and need not be repeated here.

The data of Table I are given graphically in Fig. 50, together with the curve for brother × sister and parent × offspring.

From the table and figure it is seen that with continued inbreeding according to any one of these four types the coefficient approaches the value 100. The rate of approach is different, however, in the different cases. The curves fall into two pairs. The brother × sister and the double cousin curves are precisely alike so far as concerns their curvature or shape at any given point. Similarly, the parent × offspring and single cousin curves

[3]Me. Agr. Expt. Stat. Bulletin 215, pp. 127-135.

are of the same shape. *The essential point of difference is that the cousin curves lag a generation behind the others.*

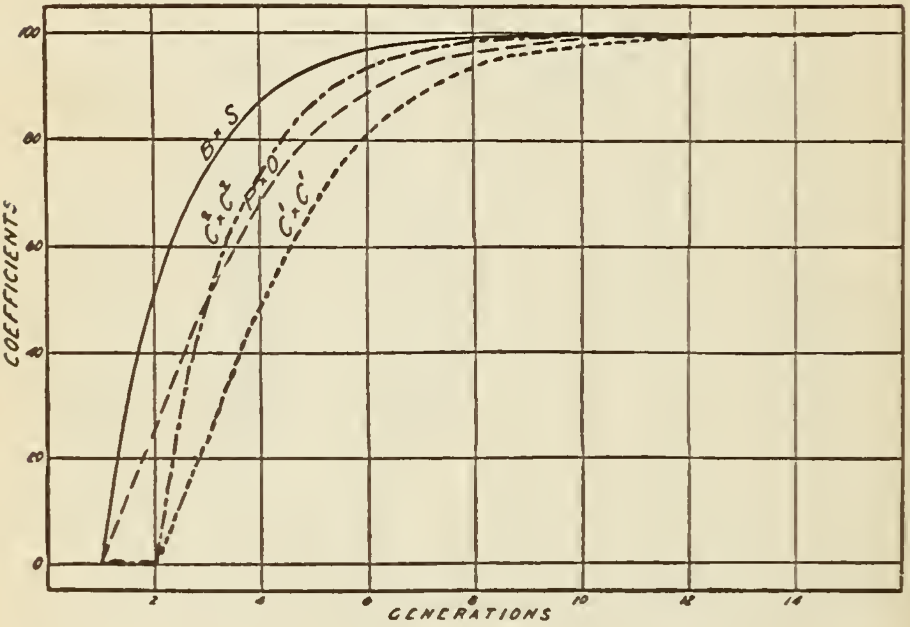


FIG. 50. Curves of inbreeding, showing (*a*) the limiting case of continued brother × sister breeding, wherein the successive coefficients of inbreeding have the maximum values; (*b*) continued parent × offspring mating; (*c*) continued first-cousin × first-cousin mating where the cousinship is double ($C^2 \times C^2$), and (*d*) continued first-cousin × first-cousin mating where the cousinship is single ($C^1 \times C^1$). The continued mating of uncle × niece gives the same curve as $C^1 \times C^1$.

## AVUNCULAR MATINGS.

We may next consider the degree of inbreeding which follows continued mating of the type uncle × niece. Pedigree Table III gives a pedigree which is of this sort. In this, as in all the other pedigrees in this paper, the upper of two bracketed individuals is regarded always as the male, and the lower as the female. Thus in Pedigree Table III individual *b* is a female, the niece of individual *a* with whom she is mated; her father *c* having been a full brother of *a*.

PEDIGREE TABLE III (HYPOTHETICAL).

*To Illustrate the Mating of Uncle × Niece.*

| | | | | | |
|---|---|---|---|---|---|
| X | *a* | *a* | *g* | *m* | *u* |
| | | | | | *v* |
| | | | | *n* | *w* |
| | | | | | *y* |
| | | | *h* | *o* | *m* |
| | | | | | *n* |
| | | | | *p* | *z* |
| | | | | | *l* |
| | | *d* | *i* | *g* | *m* |
| | | | | | *n* |
| | | | | *h* | *o* |
| | | | | | *p* |
| | | | *j* | *q* | *g* |
| | | | | | *h* |
| | | | | *r* | 2 |
| | | | | | 3 |
| | *b* | *e* | *c* | *g* | *m* |
| | | | | | *n* |
| | | | | *h* | *o* |
| | | | | | *p* |
| | | | *d* | *i* | *g* |
| | | | | | *h* |
| | | | | *j* | *q* |
| | | | | | *r* |
| | | *f* | *k* | *c* | *g* |
| | | | | | *h* |
| | | | | *d* | *i* |
| | | | | | *j* |
| | | | *l* | *s* | *c* |
| | | | | | *d* |
| | | | | *t* | 4 |
| | | | | | 5 |
| Generation number | 1 | 2 | 3 | 4 | 5 |

The values of the coefficients of inbreeding for uncle × niece mating are given in Table 2.

TABLE 2.

*Values of Coefficients of Inbreeding for Continued Uncle × Niece Mating.*

| Coefficient | Number of Ancestral Generations | Value of Coefficient |
|---|---|---|
| $Z_0$ | 1 | 0 |
| $Z_1$ | 2 | 0 |
| $Z_2$ | 3 | 25.00 |
| $Z_3$ | 4 | 50.00 |
| $Z_4$ | 5 | 68.75 |
| $Z_5$ | 6 | 81.25 |
| etc. | etc. | etc. as in Table I |

From this table it appears that the values of the coefficients of inbreeding will be exactly the same for this type of mating as in the case of single cousin mating. In other words the inbreeding is of the same degree of intensity if uncle is bred with niece, or nephew with aunt, as if single first cousins are mated together.

From the data presented in this and former papers it is clear that inbreeding continued for about ten generations, quite regardless of the type of mating, provided only it be continuously followed, leads to within one or two per cent. of complete "concentration of blood." The bearing of this result upon the general question of the degree of inbreeding which exists in the ancestry of our domestic animals today is obvious. To consider but a single case: In 1789[4] a law was passed prohibiting the importation of cattle into the Island of Jersey. Hence it follows that all pure-bred Jersey cattle of the present time must be of the descendants of the relatively few animals on the Island in 1790. Taking three years as about the average generation interval in cattle, this means about forty generations since the Island was closed to importation. The concentration of lines of descent which must have occurred in this time merely by the dropping of lines and quite regardless of the type of mating is obvious. This is not the place to go in detail into the discussion of inbreeding in Jerseys, especially as the writer hopes shortly to publish the results of an extensive study of this matter, but it seems desirable to emphasize the bearing of such hypothetical pedigrees for particular types of mating as are given in this and earlier papers, on the general problem of inbreeding.

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[4]Teste Rees's Encyclopedia and H. S. Redfield. Natl. Stockman and Farmer, December 15, 1892.

## Inbreeding and Relationship Coefficients.

The pedigree of an individual consists of two halves. One of these halves is made up of the sire and his ancestors; the other of the dam and her ancestors. Following the conception of inbreeding set forth in detail in the earlier papers of this series it is plain that the values of the coefficients of inbreeding for a particular pedigree are composed of the following elements.

1. The occurrence of the same individual animals more than once on the sire's side of the pedigree only.
2. The occurrence of the same individual animals more than once on the dam's side of the pedigree only.
3. The reappearance of animals which appear first on one side of the pedigree (either the sire's or the dam's) on the other side.

If only 1 and 2 are to be found in the pedigree it means that the sire and the dam are totally unrelated (within the limits covered by the pedigree in the particular case). On the other hand, the occurrence of 3 means that sire and dam are in some degree related, and that a portion of the observed inbreeding arises because of that fact. Now the coefficients of inbreeding, in and of themselves, tell nothing about what proportionate part has been played by these three elements in reaching the final result. It is a matter of great importance to have information on this point because of its genetic significance. It is the purpose of the present discussion to describe a general method for obtaining this desired information.

The first step in the method, stated briefly, is to break up the pedigree elimination table formed to get the successive values of $p_{n+1} - q_{n+1}$, in our former notation, into four different parts. One of these parts will include the primary reappearance on the sire's side of the pedigree of such animals as appear first on the same side This may be called the "male only" table. The second part will include the primary reappearance on the dam's side of such animals as first appear on the same side. This is the "female only" table. The third part will include the primary reappearance on the dam's side of such animals as first appear on the sire's side. The fourth part is the reverse

of the third. These last two may be called the "cross tables." The sums of the totals of these partial tables will give the total $p_{n+1} - q_{n+1}$ values for the successive generations.

The formation of the tables on this plan may be illustrated with some examples. These examples will also show the skeleton method of writing pedigree elimination tables, which saves much labor. This was referred to, but not significantly illustrated, in the earlier bulletin. It consists simply in doubling the total of the column for each generation rather than the separate items.

TABLE 3.

*Partial Pedigree Elimination Table for King Melia Rioter 14th Showing the Primary Reappearances on the Sire's Side of the Pedigree of Animals which first Appear on that Side.*

| Generation | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Melia Ann's Son | | | 1 | (2)[5] | | | | | | | |
| Melia Ann 3d | | | | 1 | (6)[5] | | | | | | |
| Lucy's Stoke Pogis | | | | | 3 | | | | | | |
| Melia Ann | | | | | 2 | | | | | | |
| St. Lambert Boy | | | | | 1 | | | | | | |
| Letty Rioter | | | | | 1 | | | | | | |
| Allie of St. Lambert | | | | | 1 | | | | | | |
| Lord Aylmer | | | | | 1 | | | | | | |
| Amelia 2d | | | | | 1 | (32)[5] | | | | | |
| Victor Hugo | | | | | | 1 | | | | | |
| Oakland's Nora | | | | | | 1 | | | | | |
| Stoke Pogis 3d | | | | | | 1 | | | | | |
| Bachelor of St. Lambert | | | | | | 1 | | | | | |
| Sir George of St. Lambert | | | | | | 1 | | | | | |
| Diana's Rioter | | | | | | 1 | | | | | |
| Orloff | | | | | | 1 | | | | | |
| Lorne | | | | | | 1 | | | | | |
| Hugo's Victoria | | | | | | 1 | (82)[5] | | | | |
| Victor Hugo | | | | | | | 1 | | | | |
| Pauline | | | | | | | 1 | | | | |
| Canada's John Bull | | | | | | | 1 | | | | |
| Oakland's Nora | | | | | | | 1 | | | | |
| Stoke Pogis 3d | | | | | | | 7 | | | | |
| Kathleen of St. Lambert | | | | | | | 1 | | | | |
| Lord Lisgar | | | | | | | 4 | | | | |
| Lucy of St. Lambert | | | | | | | 2 | | | | |
| Diana of St. Lambert | | | | | | | 1 | | | | |
| Pet of St. Lambert | | | | | | | 1 | | | | |
| Orloff | | | | | | | 1 | | | | |
| Bachelor of St. Lambert | | | | | | | 1 | | | | |
| Ida of St. Lambert | | | | | | | 1 | (210) | | | |
| Victor Hugo | | | | | | | | 2 | | | |
| Stoke Pogis 3d | | | | | | | | 2 | | | |
| Lord Lisgar | | | | | | | | 3 | | | |
| Lorne | | | | | | | | 1 | | | |
| Amelia | | | | | | | | 1 | (438)[5] | | |
| Lord Lisgar | | | | | | | | | 1 | | |
| Pride of Windsor | | | | | | | | | 2 | | |
| Laval | | | | | | | | | 1 | | |
| Amelia | | | | | | | | | 2 | | |
| Victor Hugo | | | | | | | | | 3 | (894)[5] | |
| Laval | | | | | | | | | | 1 | |
| Amelia | | | | | | | | | | 1 | |
| Lisette | | | | | | | | | | 1 | |
| Berthe | | | | | | | | | | 1 | |
| Totals | | | 1 | 3 | 16 | 41 | 105 | 219 | 447 | 898 | 1,796 |

[5] In this and the following table the numbers in brackets are in each case twice the sum of the numbers in the preceding column. They represent the accumulated ancestral reduplication up to the generation in question.

The pedigree for 12 ancestral generations of the Jersey bull King Melia Rioter 14th (103901) may be taken as the first illustration.

TABLE 4.

*Partial Pedigree Elimination Table for King Melia Rioter 14th Showing the Primary Reappearances on the Dam's Side of the Pedigree of Animals which first Appear on that Side.*

| Generation ............ | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| King's Rioter Lad ..... | — | — | — | 1 | 2 | 4 | 8 | 16 | 32 | 64 | 128 |

Table 5 is clearly the one which demands special attention. As will shortly appear, it is the most important for the theory of inbreeding. Let us attempt its analysis. Just what does the first entry mean genetically? It states that King Melia Rioter, an animal which first appeared on the sire's side of the pedigree, reappeared in the second ancestral generation on the dam's

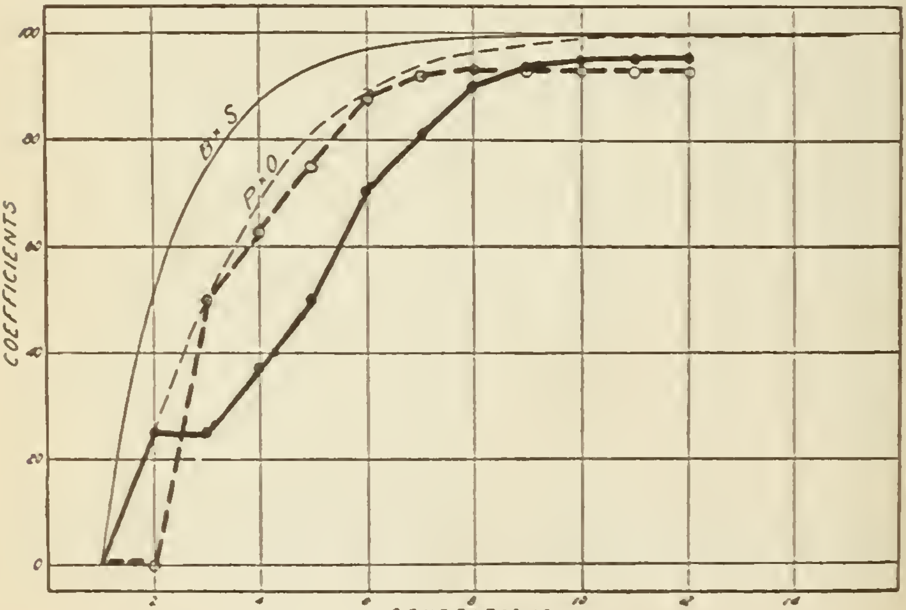


FIG. 51. Diagram showing ($a$) the total inbreeding (heavy solid line) and ($b$) the relationship (heavy broken line) curves for the Jersey bull, King Melia Rioter 14th. The high order of the inbreeding and relationship between the sire and dam in this case is evident by comparison with the lighter lines, which give the maximum values for continued brother × sister, and parent × offspring.

side. What this clearly means is that at least one-half of all the dam's ancestors, in the third and higher ancestral generations, *are identically the same animals as are ancestors of the sire.* The next entry in Table 5 indicates that in the fourth and higher ancestral generations at least $\frac{5}{8}$ of all the dam's ancestors were the same individual animals as were also ancestors of the sire. One-half of them were the same before the reappearance of St. Lambert's Rioter King. He makes up the additional $\frac{1}{8}$ of the dam's ancestry.

TABLE 5.

*Partial Pedigree Elimination Table for King Melia Rioter 14th Showing the Primary Reappearances on the Dam's Side of the Pedigree of Animals which first Appear on the Sire's Side.*

| Generation | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| King Melia Rioter | 1 | (2) | (4) | .... | .... | .... | .... | .... | ... | ... | .... |
| St. Lambert's Rioter King | .. | ... | 1 | (10) | .... | .... | .... | .... | ... | ... | .... |
| King of St. Lambert | .. | ... | ... | 1 | .... | .... | .... | .... | ... | ... | .... |
| St. Lambert Boy | .. | ... | ... | 1 | (24) | .... | .... | .... | ... | ... | .... |
| St. Lambert Boy | .. | ... | ... | .... | 2 | .... | .... | .... | ... | ... | .... |
| Oakland's Nora | .. | ... | ... | .... | 1 | .... | .... | .... | ... | ... | .... |
| St. Lambert's Rioter King | .. | ... | ... | .... | 1 | (56) | .... | .... | ... | ... | .... |
| St. Lambert Boy | .. | ... | ... | .... | .... | 1 | .... | .... | ... | ... | .... |
| King of St. Lambert | .. | ... | ... | .... | .... | 1 | .... | .... | ... | ... | .... |
| St. Lambert's Letty | .. | ... | ... | .... | .... | 1 | (118) | .... | ... | ... | .... |
| Letty Coles 2d | .. | ... | ... | .... | .... | .... | 1 | (238) | ... | ... | .... |
| King of St. Lambert | .. | ... | ... | .... | .... | .... | .... | 1 | ... | ... | .... |
| Louise's Grace | .. | ... | ... | .... | .... | .... | .... | 1 | ... | ... | .... |
| Totals | 1 | 2 | 5 | 12 | 28 | 59 | 119 | 240 | 480 | 960 | 1,920 |

From these tables it is obvious that a very considerable portion of the inbreeding shown in the pedigree of King Melia Rioter 14th arises from the fact that his sire and dam were closely related. Furthermore, both sire and dam are closely inbred in their own lines. The curve of total inbreeding in this case is shown in Fig. 51, along with the curves for continued brother $\times$ sister, and parent by offspring.

TABLE 6.

*Summarized Pedigree Elimination Table for King Melia Rioter 14th.*

| Generation | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ♂ only | | | 1 | 3 | 16 | 41 | 105 | 219 | 447 | 898 | 1,796 |
| ♀ only | | | | 1 | 2 | 4 | 8 | 16 | 32 | 64 | 128 |
| Cross-over | 1 | 2 | 5 | 12 | 28 | 59 | 119 | 240 | 480 | 960 | 1,920 |
| Together | 1 | 2 | 6 | 16 | 46 | 104 | 232 | 475 | 959 | 1,922 | 3,844 |

From this we have, for the inbreeding coefficients,

$$
\begin{aligned}
Z_0 &= 0\\
Z_1 &= 25.00\\
Z_2 &= 25.00\\
Z_3 &= 37.50\\
Z_4 &= 50.00\\
Z_5 &= 71.88\\
Z_6 &= 81.25\\
Z_7 &= 90.63\\
Z_8 &= 92.77\\
Z_9 &= 93.65\\
Z_{10} &= 93.85\\
Z_{11} &= 93.85
\end{aligned}
$$

PEDIGREE TABLE IV.

*Pedigree for Four Ancestral Generations of King Melia Rioter 14th.*

| | | | | |
|---|---|---|---|---|
| Sex ♂ King Melia Rioter 14th No. 103991 | ♂ King Melia Rioter No. 73104 | No. 63200 ♂ Marjorie Melia Ann's Son. | No. 56581 ♂ Melia Ann's King. | No. 22041 ♂ Melia Ann's Son |
| | | | | No. 100775 ♀ Lottie Melia Ann. |
| | | | No. 157263 ♀ Marjorie Melia Ann. | No. 22041 ♂ ● Melia Ann's Son. |
| | | | | No. 95883 ♀ Mary Melia Ann |
| | | No. 181544 ♀ Letty Silver Hair | No. 58169 ♂ King of All Kings | No. 54896 ♂ St. Lambert's Rioter King |
| | | | | No 114804 ♀ St Lambert's Letty |
| | | | No. 148456 ♀ Exile's Silver Hair. | No. 32559 ♂ Exile of St. Anne's |
| | | | | No. 60449 ♀ Silver Hair 4th. |
| | ♀ Larissa Marie. No. 262926 | No. 73104 ♂ ● King Melia Rioter. | No. 63200 ♂ Marjorie Melia Ann's Son. | No. 56581 ♂ § Melia Ann's King |
| | | | | No. 157263 ♀ Marjorie Melia Ann. |
| | | | No. 181544 ♀ Letty Silver Hair. | No. 58169 ♂ § King of All Kings. |
| | | | | No. 148456 ♀ § Exile's Silver Hair |
| | | No. 219360 ♀ Dula Riotress Maid. | No. 62098 ♂ King Rioter's Lad. | No. 54896 ♂ ● St. Lambert's Rioter King |
| | | | | No. 142296 ♀ King's Riotress Nora. |
| | | | No. 218796 ♀ St. Lambert's Dula Riotress. | No. 57778 ♂ St. Lambert's Boy. |
| | | | | No 174761 ♀ Rioter Lad's First Daughter |

These facts will possibly be made clearer to those not actually working much with pedigrees by Pedigree Table IV, which gives the first four ancestral generations[6] of the pedigree of King Melia Rioter 14th.

Generalizing the above reasoning we get the following result.

In $A_3$, and higher ancestral generations, 2-4 = 50.00 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In $A_4$, and higher ancestral generations, 5-8 = 62.50 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In $A_5$, and higher ancestral generations, 12-16 = 75.00 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In $A_6$, and higher ancestral generations, 28-32 = 87.50 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In $A_7$, and higher ancestral generations, 59-64 = 92.19 per cent. of the dam's ancestors are animals which are also ancestors of the sire, and so on.

These percentages are quantities of a good deal of interest. They measure the degree in which King Melia Rioter 14th's sire and dam were related to each other. Community of ancestry is the basis of kinship.

Percentages derived in the way shown above, from cross pedigree elimination tables, I have proposed to call *coefficients* of relationship, and to designate by the letter $K$, with appropriate sub-numbers referring to the generation. These relationship coefficients are, with some limitations, independent of the inbreeding coefficients in the values they may take, though the two will usually be correlated to some degree. It is, however, possible to have a high value of $Z$ with $K = 0$.

---

[6]In the study of pedigrees stress is naturally laid on the ancestral generations, rather than on the filial, as in breeding experiments. It becomes very convenient to have a brief designation for ancestral generations, in the same way that $F_1$, $F_2$, etc., are used to denote filial generations. I would suggest the use of the letter A with sub-numbers for this purpose. We then have $A_1$ denoting the parental generation, $A_2$ the grandparental, $A_3$ the great-grandparental, etc.

TABLE 7.

*Comparing the Maximum Possible Values of the Coefficients of Inbreeding (Z) when the Coefficient of Relationship K Equals (a) Zero, and (b) 100.*

| Generation | Maximum Possible Value of $Z$ when $K = 0$ | Maximum Possible Value of $Z$ when $K = 100$ |
|---|---|---|
| $A_1$ | 0 | 0 |
| $A_2$ | 0 | 50.00 |
| $A_3$ | 50.00 | 75.00 |
| $A_4$ | 75.00 | 87.50 |
| $A_5$ | 87.50 | 93.75 |
| $A_6$ | 93.75 | 96.88 |
| $A_7$ | 96.88 | 98.44 |
| $A_8$ | 98.44 | 99.22 |
| $A_9$ | 99.22 | 99.61 |
| $A_{10}$ | 99.61 | 99.80 |

The most important feature of the relationship coefficients is found in their genetic implications. This can be indicated best by an illustration. Let us consider the case of the maximum possible degree of inbreeding with $K = 0$. This will be found when the sire and the dam are each inbred to the highest possible degree (continued brother $\times$ sister mating) but are in no way related to each other. Such a case would be afforded, for example, if a Jersey bull, the product of continued brother $\times$ sister mating, was bred to a Holstein cow, which was also the product of a continued brother by sister breeding. Clearly $K$ would be 0, since no animal on one half of the pedigree could even appear on the other. The values of the successive coefficients of inbreeding ($Z$'s) in such a case are shown in Table 7, where they are compared with the coefficients of inbreeding in complete continued brother $\times$ sister mating, where $K = 100$.[1]

*From this it appears that an individual may be inbred in 10 generations to within two-tenths of one per cent. as intensely, measured by the coefficients of inbreeding, if his sire and dam are in no way related, as he would be if his sire and dam were brother and sister.* But clearly the germinal constitution of the individual produced would, except by the most remote chance, be quite different in the two cases.

---

[1]Since, of course, *all* of a sister's ancestors are identical with her brother's.

It is suggested that the two constants be written together for each generation, the coefficient of inbreeding being followed by the coefficient of relationship in brackets. Thus we have

INBREEDING AND RELATIONSHIP COEFFICIENTS OF KING MELIA RIOTER 14TH.

$$
\begin{array}{lll}
Z_0\,(K_1) = & 0 & (0) \\
Z_1\,(K_2) = & 25 & (0) \\
Z_2\,(K_3) = & 25.00 & (50.00) \\
Z_3\,(K_4) = & 37.50 & (62.50) \\
Z_4\,(K_5) = & 50.00 & (75.00) \\
Z_5\,(K_6) = & 71.88 & (87.50) \\
Z_6\,(K_7) = & 81.25 & (92.19) \\
Z_7\,(K_8) = & 90.63 & (92.97) \\
Z_8\,(K_9) = & 92.77 & (93.75) \\
Z_9\,(K_{10}) = & 93.65 & (93.75) \\
Z_{10}(K_{11}) = & 93.85 & (93.75) \\
Z_{11}(K_{12}) = & 93.85 & (93.75)
\end{array}
$$

The physical meaning of these expressions is simple and straightforward. $Z_4\ (K_5)$ tells us that in the 5th ancestral generation of King Melia Rioter 14th he had only one-half as many different ancestors as was possible for that generation, and of his ancestors three-fourths were common to his sire and his dam. However one looks at the matter there can be no denial that King Melia Rioter 14th is a closely inbred animal.

In Fig. 51 the heavy broken line gives the relationship coefficients for King Melia Rioter 14th. It will be instructive now to consider another example by way of contrast. Again a Jersey bull, Blossom's Glorene (102701), will be taken. Only the final result need be given.

INBREEDING AND RELATIONSHIP COEFFICIENTS OF BLOSSOM'S GLORENE.

$$
\begin{array}{lll}
Z_0(K_1) = & 0 & (0) \\
Z_1(K_2) = & 0 & (0) \\
Z_2(K_3) = & 12.50 & (0) \\
Z_3(K_4) = & 12.50 & (0) \\
Z_4(K_5) = & 25.00 & (0) \\
Z_5(K_6) = & 29.69 & (0) \\
Z_6(K_7) = & 35.94 & (0) \\
Z_7(K_8) = & 40.23 & (0)
\end{array}
$$

The total inbreeding and the relationship curves are given in Fig. 52.

The difference in the breeding of this bull and the one considered in the former example is striking. In the 8th ancestral generation Blossom's Glorene has but 60 per cent. of the num-

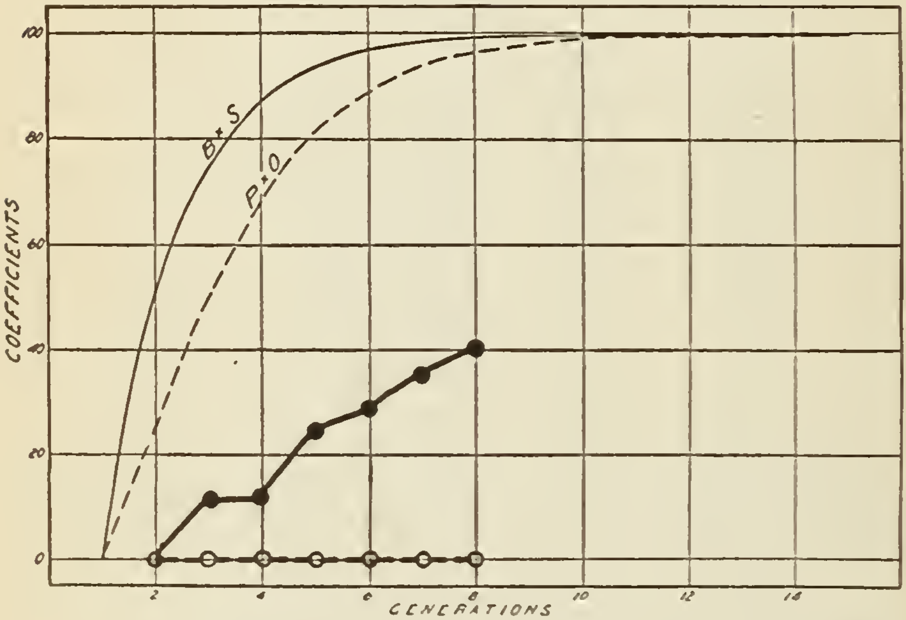


FIG. 52. Diagram showing the total inbreeding (heavy solid line) and the relationship (heavy broken line) curves for the Jersey bull Blossom's Glorene, over a period of eight ancestral generations. Compare with Fig. 51.

ber of different ancestors possible in that generation, but not one single animal in the ancestry of his sire occurs in the ancestry of his dam (within the limits $A_1$ to $A_8$). The probability is that Blossom's Glorene is heterozygous in respect of many of his characters, while King Melia Rioter 14th is homozygous.

The pedigree of Blossom's Glorene is shown in Pedigree Table V.

## PEDIGREE TABLE V.

*Pedigree for Four Ancestral Generations of Blossom's Glorene.*

| | | | | |
|---|---|---|---|---|
| Sex ♂ No. 102701 Blossom's Glorene | ♂ No. 86163 Dan of Peach Hill Farm. | No. 66900 ♂ Golden Lad's Double Grandson. | No. 53960 ♂ Golden Lad's Successor. | No. P. S. 2153 J. H. B. Great Scot. (Imp.) ♂ |
| | | | | No. 127228 Golden Ora. ♀ |
| | | | No. 149149 ♀ Golden May of St. Peter. | No. P. S. 1242 J. H. B. Golden Lad. ♂ |
| | | | | No. F. S. 7983 J. H. B. Cornflower. ♀ |
| | | No. 99742 ♀ Oxorilletta 2d. | No. 23472 ♂ Glorene's Prince. | No. 10401 King Eric. ♂ |
| | | | | No. 4785. Glorene. ♀ |
| | | | No. 50983 ♀ Oxorilletta. | No. 17417 Oxori. ♂ |
| | | | | No. 26838. Orinoque's Riletta. ♀ |
| | ♀ No. 235288 Blossom of Peach Hill Farm. | No. 84318. ♂ Oyama of Peach Hill Farm. | No. 55317. ♂ Pedro of Valley Home 2d. | No. 48886. Pedro of Valley Home. ♂ |
| | | | | No. 97523. Madeline Pollard. ♀ |
| | | | No. 132053. ♀ Bessie of Highland. | No. 31111. Essie W's. Rioter. ♂ |
| | | | | No. 113949 Lena of High Land. ♀ |
| | | No. 230006 ♀ Lillie of Peach Hill Farm. | No. 55317 ♂ ● Pedro of Valley Home 2d. | No. 48886. ⊗ Pedro of Valley Home. ♂ |
| | | | | No. 97523. ⊗ Madeline Pollard. ♀ |
| | | | No. 179056. ♀ Spotty Bouquet. | No. 46717. Silver Spray Pogis ♂ |
| | | | | No. 114910. Charm of Bouquet. ♀ |

From this table it will be seen that this bull Blossom's Glorene essentially represents a cross of Island stock on St. Lambert. His sire is strong in Island blood particularly that of the famous bull Golden Lad P. S. 1242. The American blood on the sire's side is *not* St. Lambert. These facts make plain why it is that we get the values for inbreeding and relationship coefficients which have been shown above.

In view of the very marked difference between the two Jersey bulls which have been used as examples in the above discussion, King Melia Rioter 14th (103901) and Blossom's Glorene (102701), it becomes of interest to learn something, if possible, about the animals themselves. An attempt has been made to do

this, by correspondence with the American Jersey Cattle Club, and the breeders and various owners of the animals under consideration.[5]

Let us first consider the registered progeny of these bulls. These are shown in Table 8.

TABLE 8.

*Registered Progeny of King Melia Rioter 14th and Blossom's Glorene.*

| KING MELIA RIOTER 14TH (103901) | | | BLOSSOM'S GLORENE (102701) | | |
|---|---|---|---|---|---|
| Sex. | Name. | Number | Sex. | Name. | Number |
| Male | Mary's Jolly Raven. | 131203 | Female | Sadie Glorene. | 296356 |
| | | | Female | Maggie Lambert Blossom | 318657 |
| | | | Female | Glorene's Damsel. | 335348 |
| | | | Female | Rose Glorene | 335349 |
| | | | Female | Freda Glorene | 335351 |
| | | | Female | Edith Glorene. | 335352 |
| | | | Female | Glorene's Loretta D | 335353 |
| | | | Female | Golden Lad's Miss Glorene. | 335354 |
| | | | Female | Queen Ola Bess | 335355 |
| | | | Female | Glorene's Burletta. | 335358 |

From the table it might appear that Blossom's Glorene was a much surer breeder than King Melia Rioter 14th. This, however, was not in fact the case. The difference in the two halves of the table only means that more of the progeny of the former bull than of the latter *were registered*. I am informed by Mr. S. B. McCague, who was the owner of King Melia Rioter 14th during the major portion of his breeding life, that he was a sure calf getter. Mr. McCague now has a good deal of stock from him eligible to registration, but not registered.

Regarding the characteristics of the two animals, it appears from the available evidence that both were excellent bulls, of fine conformation and high constitutional vigor. Unfortunately it is not now possible to get a photograph of either animal. Figures 53 and 54 give illustrations of certain of the progeny of

[5]For aid in this inquiry we are particularly indebted to Mr. R. M. Gow, Secretary of the American Jersey Cattle Club, who in this as in other matters has always been most kind in furnishing data from the records of the Club; to Mr. W. J. Hussey, of Mt. Pleasant, Ohio, Mr. S. B. McCague, of Coraopolis, Pa., Mr. J. T. Ward, of Rogers, Ohio, and Mr. John K. Kelly, of Kensington, Ohio.

King Melia Rioter 14th. This is the most interesting, because he was such an extremely inbred animal. The photographs were furnished by Mr. McCague. They leave something to be desired so far as posing is concerned, but still give a very fair idea regarding these calves.

Fig. 53. Showing two daughters and a grand-daughter of King Melia Rioter 14th.

It is clear from these photographs, and the statements of the owners, that in spite of the excessive inbreeding these animals are not degenerate weaklings. King Melia Rioter 14th was as a calf a very superior animal, according to the statement of W. G. Hussey, a Jersey breeder of long experience. Mr. McCague, who owned him as an adult, says that he "was a splendid animal of fine conformation." He was sold about a year ago. Mr. McCague states that "the party who bought him, through improper handling made him cross, and he killed him."

Regarding Blossom's Glorene, the breeder, Mr. J. T. Ward, of Rogers, Ohio, writes as follows: "I sold the bull which you are interested about when he was a calf. Have not seen him since but he was a dandy when a calf . . . Enclosed you will find a picture of his sire. The young bull should have

proven as good or better than his sire." The photograph referred to is reproduced here as Fig. 55.

FIG. 54. King's King Melia, *aet.* 7 months, a son of King Melia Rioter 14th, out of Meadow Brook Edna (283141).

The last owner of this animal, Mr. J. J. Kelley of Kensington, Ohio, states that as an adult he fulfilled the promise he made as a calf and was a first-class bull. He was a sure breeder, getting stock of good quality. He was disposed of "owing to his vicious disposition."

It may fairly be said in conclusion that there does not appear to be any outstanding or marked difference between the two bulls, King Melia Rioter 14th, and Blossom's Glorene, in respect of either (a) constitutional vigor, (b) breeding ability, (c) conformation, or (d) quality of get. So far as these qualities, at least, are concerned there are no differences between these animals in any way corresponding in either degree or kind to the

differences which we have seen to exist in their pedigrees in respect of the degree and nature of the inbreeding there existing. These facts constitute a definite, though small, bit of evi-

Fig. 55. Photograph of the sire of Blossom's Glorene, Don of Peach Hill Farm (86163).

dence in favor of the view, which finds much support in the literature of both practical stock breeding and experimental genetics, that the degree of inbreeding, *in and of itself alone,* has very little directly to do with the qualities of the offspring.

## Summary.

This bulletin is a continuation of Bulletin 215 of this Station. In it the subject of continued cousin mating and continued mating of the avuncular type are first discussed. It is shown that all types of cousin and avuncular matings if continued lead to values of the coefficient of inbreeding approaching 100 per cent.

Relationship coefficients and the method of calculating them are described. As illustrations of method the pedigrees of two Jersey bulls, King Melia Rioter 14th and Blossom's Glorene, are discussed. Following this the available data regarding these animals and their progeny are presented.